ANIMAL ACTIVITY IN SOILS AS A DECISIVE FACTOR IN ESTABLISHMENT OF HUMUS FORMS

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Comparative micromorphological studies of thin sections give a surprisingly clear insight into the kind and rate of soil activity, primarily in regard to decomposition and humification. It is easy to show that the activity of soil animals has such a decisive influence on the composition and the structure of the humus horizons that it must be considered to be the most important criterion for the definition and classification of the different humus forms.

Since the time of Hampus von Post and P. E. Müller the idea of humus form has proved to be one of the most valuable concepts for the study of soils, particularly in the last decades. The term ' humus form ' was created by Müller in 1879. His approach to the investigation of soils was so entirely new for his time that Müller can be regarded with W. W. Dokuchaev, whose main work appeared in the same year, as one of the great founders of modern soil typology or modern pedology in general. His idea of ' humus form ' is not a chemical concept and therefore does not mean merely a particular organic substance or a group of organic substances. It is not confined to the so-called ' humus substances ', nor even to the ' organic matter ' of the soil since it comprises also the inorganic matter and the way in which the organic and inorganic constituents are mixed or combined with one another. In addition to this, the ' humus form ' is bound up with the formation of a typical humus profile and with a typical ' soil life ' produced by typical microbial and macrobial biotic communities and their activities. The ' humus form ' is thus a concept of a formation in nature: that is to say, a complex consisting of the biotic community plus its biotope. It is a concept of a formation in nature like that of the soil as a whole, of which the ' humus form ' is a part. In terms of the usual profile nomenclature it comprises more or less the ' living ' A horizon plus the L layer on its surface, although no humus form could be thought of without the connexion with the remaining parts of the soil and the interrelation between life and dynamics of both.

While Hampus von Post has given us the main concepts of the

subaqueous humus forms, Müller has created the three main concepts of terrestrial humus forms which are still in use today. He has not only given us the concepts of 'mor' and 'mull' but also the concept of the third main humus form which a quarter of a century later came into use under the name of 'moder'. This moder concept, the identity of which with the concept of Müller is evident from his careful description, was named by him as 'insect mull' or 'mull-like mor'. From this way of naming it can be seen that he regarded this particular humus form as belonging neither to the true mull nor to the true mor but to a third form between the two. It is important to soil zoology that both investigators, Müller and von Post, had already recognized the great importance that animal activity plays in the establishment of humus forms and they made use of this fact in their descriptions and definitions.

At the time of Müller soil zoology, as a special branch of soil biology, did not exist. Even the knowledge of the great variability of the soil and its classification was in its infancy. When in 1949, 70 years after the first edition of Müller's book, I tried to bring together all our present knowledge by writing my book *The Soils of Europe*, I was able to describe already 30 well definable humus forms, that is, 16 main forms and 14 varieties and subvarieties. The use of the thin section technique made it possible to me to apply detailed micromorphological characters for their definition in addition to profile differences and macromorphological characters. There exists no variety or subvariety in which the special influence of animal activity is not visible or is not most characteristic. Detailed information on the genesis of the many varieties of humus formation given by the soil zoologist is therefore of greatest importance, not only for soil morphology and soil systematics, but also for the general understanding of the biology of different soils.

In view of this great importance it was decided to show to the audience of this Easter School a number of photomicrographs of a series of very different humus forms in order to put forward some suggestions and initiate immediate or later discussions on particular soil problems or perhaps to bring about some personal collaboration. The very recent coloured lantern-slides shown were mostly of thin sections of humus formations; they had not hitherto been published or shown elsewhere. A selection of them is reproduced here in black and white (*Figures 12–23*).

In attempting to generalize my direct observations on the subject, as a result of continuous investigations of living humus formations found in many different parts of the world and their thin sections

Figure 12—Raw humus from tropical iron humus podzol, Yangambi, Belgian Congo. Little-decomposed plant remains with preserved cell structure. At the left, feeding cavity with droppings of Oribatid mites. [The interior of the droppings actually shows almost the same ochre-brown colour as the surrounding plant remains, indicating low decomposition and humification.] × 50.

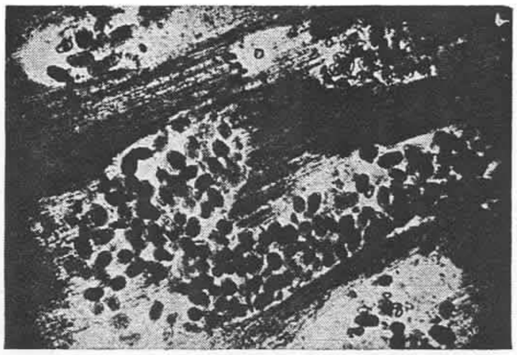

Figure 13—Syrozem humus in carbonate raw soil (white rendzina), Sierra grossa, Spain. Fragments of little-decomposed plant remains tightly embedded in a white, very calcareous marl. Numerous rounded feeding cavities filled with abundant Oribatid droppings. These mites are capable of attacking raw plant remains. The droppings show little decomposition and humification. × 30.

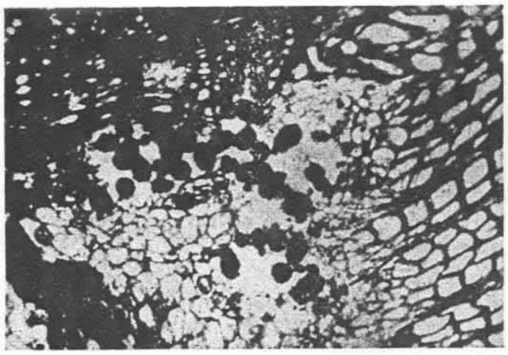

Figure 14—Raw peat invaded by small terrestrial arthropods. Thin section from dolomite nodule in carboniferous coal seam, Dulesgate. Well preserved plant remains of Lepidostrobus with feeding cavity containing animal droppings. Up to now this is the oldest datable evidence of the attack of plant residues by a terrestrial fauna. × 33.

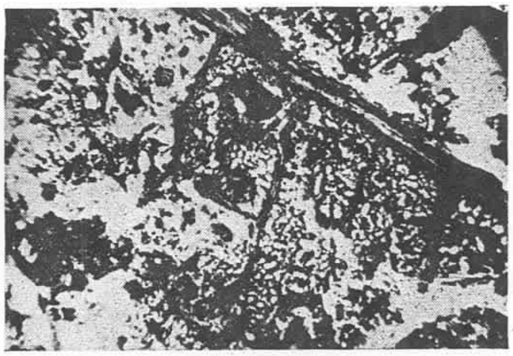

Figure 15—F horizon of moder, Valle de Roncal, Pyrenees. Remains of a birch leaf skeletonized by the action of small arthropods which feed on the soft parts and do not attack the hard and fibrous tissues. × 25.

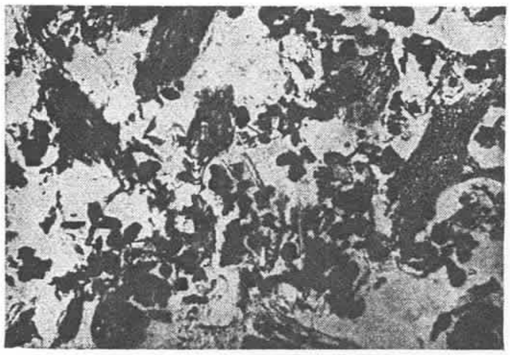

Figure 16—Acid alpine silicate moder, Hohe Tauern, Austria. Loose mixture of blackish droppings of small arthropods (showing good humification), little-decomposed fragments of plant remains and mineral grains. [The plant fragments have a vivid reddish colour frequent in raw-humus and dystrophic moder varieties.]

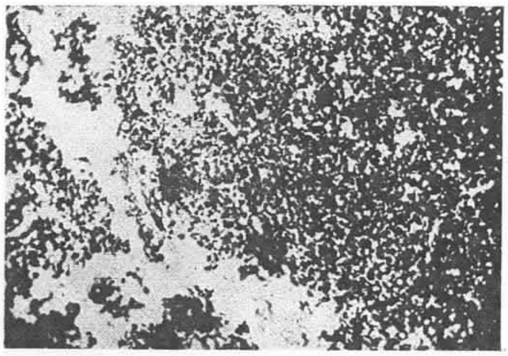

Figure 17—Alpine pitch moder on triassic limestone, Dachstein, Austria. In this blackish moder of a pitch-like appearance all organic residues have been transformed into small blackish cylindrical droppings, presumably in the first place of Collembola which greatly dominate in the animal population. × 20.

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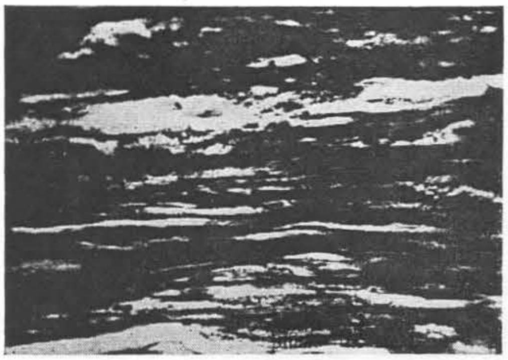

Figure 18—Birch carr peat, Bohemian Forest. The fibrous remains of birch wood show little decomposition and humification. [Their colour is a striking reddish brown, frequent in acid wood peats.] ×30.

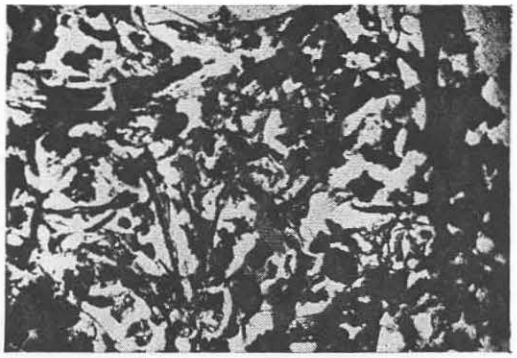

Figure 19—The same birch carr peat with beginning moder formation in the surface layer. This is shown by the entangling of the fibrous plant remains and by increasing deposition of blackish-brown droppings of small arthropods (mostly mites and Collembola), showing fairly good humification. ×30.

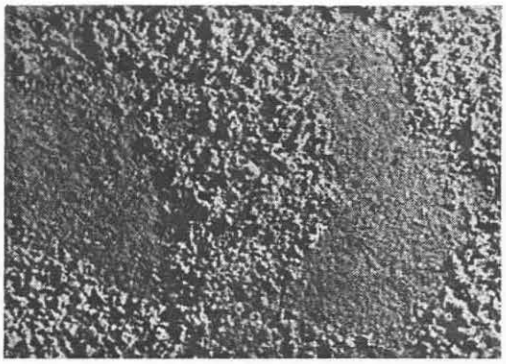

Figure 20—Soil surface of a culture enriched by Enchytraeidae, showing accumulations of their droppings (Photograph: Miss M. Trappmann).

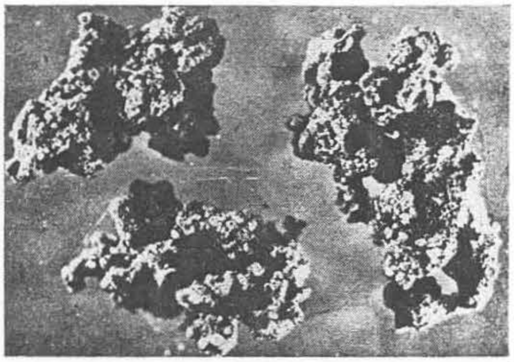

Figure 21—Single dropping complexes of Enchytraeidae enlarged and showing fragments of the micro-sponge structure frequently formed by these animals. (Photograph: Miss M. Trappmann).

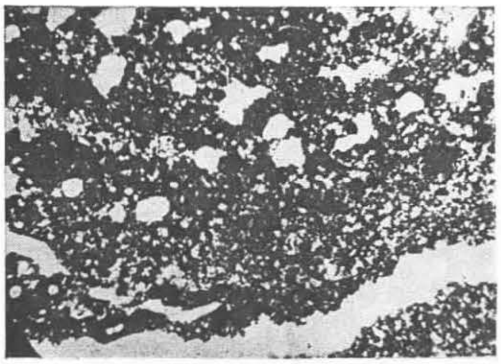

Figure 22—Micro-sponge structure in mull of Webster prairie soil, Iowa. The large white spaces are cavities, the small white spots mineral grains. No presence of plant remains; almost complete decomposition and humification. × 20.

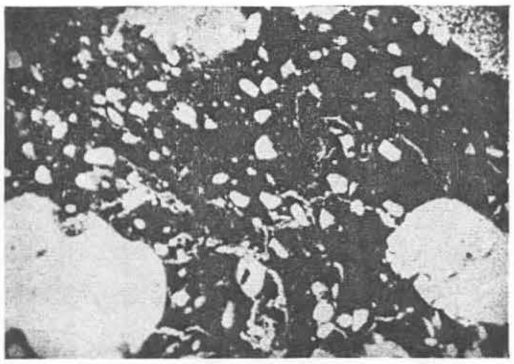

Figure 23—Termite mull near Yangambi, Belgian Congo. Well rounded quartz grains (all white parts) are embedded in a dense humous matrix of 'braunlehm' character interlaced by fine shrinking cracks. Visible plant residues are completely absent. Almost complete decomposition and humification; the humus substances are like a dye in the matrix. ×25.

during a period of a quarter of a century, I can summarize them in the following sentences:

(1) Humus formations with little animal activity show as a rule little humification.

Examples—Raw peats, syrozem humus, raw-humus, eilag humus, tangel humus.*

(2) Between the activity of the micro-flora in general and the development and activity of the soil fauna close relations exist. Fresh fibrous plant residues or residues containing substances which depress bacterial life can only be attacked by a few specialized animal forms. A strong development of fungi greatly depresses animal activity.

(3) The progress of humification moves parallel with the accumulation of animal excreta in the soil.

(4) In all highly organized humus formations, droppings of those animals which are capable of taking up large amounts of mineral particles with their food and of mixing it with organic substances greatly predominate. The mixing and binding activity cannot be replaced by any other agent in the soil.

(5) In humification and in the formation of the different humus forms the soil animals are not merely playing a kind of subsidiary role but the most decisive one.

How can the activity of the soil animals be recognized and measured ? What part of their activity is the most essential in regard to soil and humus formation ? Is knowledge of the rate of carbon dioxide production sufficient ? Are all animals found in the soil of importance for soil formation or is it a comparatively small group in each particular case which are specially active in creating different humus forms ?

The part of animal activity which can be regarded as the most important for the formation of different humus forms comprises the following items:

(1) The selective decomposition of the different parts of different organic residues.

(2) The kind and degree of humification, that is of the transformation of the different substances of the plant and animal body into humus substances.

(3) The influence of animals in the formation of particular soil structures and structure elements.

* Explanation and definition of these humus forms are given in *The Soils of Europe* (Kubiena, 1953).

By what methods can these particular modes of animal activity be recognized ? Since the soil represents one of the most complex formations in nature no more satisfactory method, which is rapid enough and gives an insight into the formations as a whole at one time, has so far been devised than microscopic investigation, particularly when applied to thin sections. The results can be presented by detailed description, by estimation of the decomposition or humification rates (very low, low, moderate, good, very good), or by quantitative measuring after the Rossival method, already applied in the investigation of rock sections.

In most cases description or estimation will be enough to obtain sufficient evidence for differentiating between the humus forms. By direct observation, in the living state, of animals isolated from the humus formations in question and by keeping these in cultures on different substrates, their particular activity may be recognized and brought into relationship with the facts given by microscopic investigation of the soil preparations. The following details seem to me to be of particular importance:

(1) Different plants and different parts of plants, such as leaves, stems, roots and particular plant tissues are attacked by different kinds of animal in different ways, so that a detailed knowledge of their mode of removing particular tissues, of forming feeding cavities, of attacking or of refusing particular plants or parts of plants will provide us with better opportunities of deducing from their mode of feeding which groups of animals are particularly active in the development of a given humus formation. This knowledge will supplement greatly the information given by the types of droppings present. Many animal groups, genera or even species have such typical forms and sizes of droppings that their activity and importance can be easily recognized by the prevalence of particular faecal types. In the interior of the droppings the kind and degree of the decomposition of the different organic remains can easily be compared with the kind and rate of decomposition of the organic remains outside the coprogenic part of a humus formation.

(2) The accumulation of dark-coloured humus substances inside the different types of faeces gives rise to the possibility of estimating also the degree of humification and of obtaining an inside view into the efficiency of different animal forms in this respect.

(3) Aggregate formation in soils is to a great part caused by soil animals. Again the knowledge of the types of droppings, by which the animals involved in the aggregate formation can be easily

recognized, is of great importance. It is necessary to recognize as far as possible even droppings which have been destroyed by fracturing or by leaching away of the peptizable substances. It is essential to have a knowledge of the efficiency of different animal groups in mixing or combining organic matter with inorganic constituents and in producing particular cementing substances which give rise to the formation of aggregates stable in water. In addition to the formation of aggregates the combination of aggregates to form different structure varieties is very much associated with different animals and our knowledge is far from being complete in this respect.

If we examine the most common terrestrial humus forms from the view-point of their most characteristic animal activity, we must of course include also those formations in which the lack of intensive animal life is the essential character. In their micromorphology, plant residues with well preserved cellular structures prevail, while animal droppings are scanty and frequently show also very incomplete decomposition and humification. In raw humus (raw mor) great acidity, development of acid humus sols and certain substances which depress bacterial life and sometimes the luxuriant development of certain fungi are the main causes for the formation; in syrozem humus it is the low state of development of soil life, in which only a few pioneer organisms have recently gained access; in eilag humus it is the frequent freezing and the powerful drying effect of strong winds in highly exposed alpine habitats. It can thus be seen from the results of their activity that there must be a special micro-flora and fauna in every case and detailed investigations would be highly desirable.

In moder (mull-like mor* of Müller) most of the plant residues are transformed into droppings of small arthropods among which, in the more primitive moder varieties, those of Collembola and Oribatid mites generally predominate. The plant residues outside the droppings are reduced to small fragments but still show their cell structures and are little humified, while humification within the animal droppings is considerable. Generally, droppings, plant fragments and mineral grains form a loose mixture. Sometimes particular net-like structures formed by irregular chains of small droppings can be found in moder which perhaps originate as a result of the transformation of fibrous plant residues into

* The term 'mor' is avoided because of its great similarity to moor (or the German 'Moor') and the continuous confusion this fact has brought about in practical usage and in the literature. For the same reason Müller's German translation 'Torf' for 'mor' is avoided.

coprogenic masses. In acid moder the shapes of the droppings are frequently destroyed by washing. In some coarse moder (the transition form to raw humus) the washed out peptizable humus substances from the droppings may act as binding substances and form a dense matted layer of the H and partly also of the F horizon. Moder can be formed, not only from forest litter, but also from raw peat, in an analogous way to forest soils, if the ground water-table of the moor is definitely lowered. Then a complete transformation of the plant residues into animal droppings may take place.

In mull-like moder, a transition form from moder to true mull, droppings of larger arthropods which are capable of absorbing great quantities of mineral substances with their food become very prevalent. Generally myriapods are much more active in this respect than insects, although these and even earthworms sometimes may exert a considerable influence in the production of moder aggregates rich in mineral grains. The difference between this humus form and the true mull is easily recognized by microscopic methods. The aggregates in mull-like moder are more or less a mechanical mixture of organic constituents with mineral particles whereby primarily humus substances act as binding material. These aggregates show only a loose form of binding, the mineral particles and organic matter being easily separated by micro-mechanical methods. For diagnostic purposes the micro-morphological aspect will be sufficient for distinguishing mull-like moder from real mull. Generally there are also some small, little decomposed plant remains left even inside the animal droppings.

The rendzina moder is distinguished from the above mentioned silicate moders by its content of lime. It contains not only small calcite or dolomite grains and, according to the rendzina variety, recrystallized calcium carbonate in different parts of the profile but also calcium humates in the humus fraction. In view of the special living conditions and the particular processes of humus formation, the separation of this humus forms from others of similar appearance is important. The shapes of the animal droppings are here well preserved as a rule. Like the silicate moder it occurs also in the mull-like form as mull-like rendzina moder with the prevalence of large droppings with a high content of calcite or dolomite grains.

In mull we have a humus form in which decomposition and humification of the organic residues is not only best advanced, but in which, due to animal activity, a mechanically inseparable complex between the humus substance and the clay substance has been formed. Plant residues showing cell structure are practically

absent. The humified organic substance is highly dispersed and absorbed by the fine fractions of the soil like a dye. Mull is a product of most favourable conditions with mild to warm soil climate, absence of waterlogging, sufficient nutrient and clay content and the presence of plant covers which yield easily decomposible residues. In Europe it is not only formed under the influence of earthworms but also of Enchytraeidae.

In soils which produce sufficient water-stable binding substances earthworms may create a spongy structure, the most favourable and desirable structure for plant production. Their activity is not only structure-forming but also structure-stabilizing, since the structure is much less readily destroyed by water. In some soils with particularly unstable binding substances, which from the beginning are very dense in all parts of their interior, the formation of a stable sponge-like structure by earthworms is rendered more difficult or even made impossible. It is in these soils, mostly of a ' braunlehm ' character, where the earthworm casts are to a great extent brought to the surface whereas in general the casts are mostly deposited within the soil. In the humid tropics where laterite layers are formed below deep coverings of ' braunlehm ', earthworms deposit their casts in enormous quantities in the cavities and channels of the laterite subsoil. These ' braunlehm ' casts gradually undergo laterization and give rise to the frequent vermicular structures in laterites. In Spanish Guinea they permit a detailed study of all phases of laterite formation.

Similar to the earthworms the Enchytraeidae also may produce sponge structures. Their influence on structure formation is less well known and deserves more intensive study. Some mull formations may show even more of these micro-sponge fabrics than those of the macro-sponge of the earthworms.

Some humus formations greatly influenced by the activity of termites, which I collected in the Belgian Congo, reveal a surprisingly good decomposition and humification. It appears that the termites prevent completely the action of earthworms, but their activity seems to have similar results. They have an even greater efficiency in stabilizing structures in soils of a ' braunlehm ' character which become, under their influence, so unaffected by rain that they are widely used for road construction in those parts of the tropical rain forest where concrete laterite material is not available.

In conclusion the following may be said. Thin sections of humus formations investigated microscopically give an image of the totality of the events which have taken place within them. The wealth of detail which is made visible in them as a result of the

activity of various organisms is inexhaustible. We can only learn to understand the whole if we learn to understand detail by detail. This can only be made possible by innumerable detailed studies by micro-biologolists and primarily by the soil zoologist. The studies should be devoted to the biology of every single organism of importance within the environment of the soil, to their particular soil-forming activity in all phases, and at the same time to the way in which the changes brought about by their activity have become visible in the micromorphology of the soil. The sum of all such information would enable us to read a soil preparation like a book. If there would be little left that we could not explain, then we would be more justified than today in saying that we know something of soils and humus formations.

DISCUSSION

MR. J. G. BLOWER: We have all learned much from Professor Kubiena. In pedology there appears to be a striking analogy with the older studies in Zoology. First there was morphology, then functional morphology, and then physiology. Physiology was at first, however, premature and lacked a full understanding of morphology for its true interpretation. It would seem that pedology was similar. The study of the physiology of soil animals is perhaps a little premature. Should we not first do a little more soil morphology — that is the describing of animals and their droppings *in situ* before we tackle physiological problems ?

PROFESSOR W. KÜHNELT: In connexion with the soil sections shown by Professor Kubiena, I should like to point out a very useful method of studying the activity of soil animals on the spot. This is simply by watching them in the field by means of a lens or a binocular microscope. In this way one can gain very much information. The information becomes more complete if the animals found are kept separately in little tubes under suitable conditions of temperature and humidity. In this way, droppings can be obtained and compared with the samples found in the soil. Finally, cultures can be set up and life-history studies of the animals carried out.

MR. O. GILBERT (Nature Conservancy, Grange-over-Sands): I would like to ask Professor Kubiena what he means by the term 'peptized' which he has used several times.

PROFESSOR KUBIENA: 'Peptized' means finely dispersed, as opposed to 'flocculated', and is used for colloids, when forming a 'sol' instead of forming a 'gel'. Peptized colloids in the soil are very mobile. Thus peptized iron hydroxide in 'braunlehm' can lead to the formation of slowly growing concretions of considerable size; flocculated iron hydroxide as in 'braunerde' remains fixed.

DR. W. A. RICHARDSON (Sutton Bonington): What exactly is the composition of the concretion occurring in the laterite shown in Professor Kubiena's remarkable photographs ? Has the earthworm any part in the

initiation or growth of these concretions, or, more generally, is there any biological activity in their production, or is it merely a matter of chemical mineralization ?

PROFESSOR KUBIENA: The iron hydroxide concretions formed in the fresh earthworm casts which are deposited in the cavities of the laterite crusts would become initiated in any similar ' braunlehm ' material under the same thoroughly balanced water conditions. They are produced by entirely non-biological processes. They are typical for the initial phase of certain laterite varieties (pisolitic laterites) but are also formed in subtropical climates, and, with relict and fossil ' braunlehm ' layers, even in temperate climates. They are fed as they grow primarily from peptized amorphous iron hydroxides, but consist for a great part of crystalline minerals. In the course of laterization these are mostly transformed by aging into haematite whereby the originally dark brown colour is changed to dazzling red.

MR. J. E. PEACHEY (Zoology Department, University of Durham): Has Professor Kubiena any evidence from his thin sections for the activities of Enchytraeidae in peat, since we now know that peat supports quite a large population of these animals ?

PROFESSOR KUBIENA: My direct knowledge on the formation of a kind of micro-sponge fabric as a result of the activity of Enchytraeidae refers only to mineral soils. I have seen similar structures in peat moder, but could not obtain any evidence whether they were formed by Enchytraeidae. Such evidence, however, would be easy to obtain by keeping a peat culture containing Enchytraeidae, by observing microscopically the activity of the animals and by preparing thin sections of the final product at the end of the experiment.

MISS S. HEPPLE (Botany Department, University of Liverpool): The nature of humus in the chemical and descriptive literature is summed up in the phrase of our chemists: ' dirty black stuff '. Yet, in soil sections, humus has a very definite reddish-brown colour. Have you any idea what causes this reddening ?

PROFESSOR KUBIENA: Half decomposed plant remnants in thin sections having the cell structures generally well preserved and showing a vivid reddish colour are frequent in humus formations in environments with ' dystrophic ' conditions, that is showing not only great lack of mineral nutrients but also abnormal living conditions (accompanied by great acidity) which are unfavourable for most micro-organisms. The reddish substances seem to belong to the group of ' humo-lignins '—transition products of incomplete humification. Where they appear, animal life in the humus is, as a rule, not very active.

MR. V. I. STEWART (Department of Soil Science, University of Aberdeen): Would Professor Kubiena say that one can get laterization without the presence of earthworms ?

PROFESSOR KUBIENA: Earthworms are not responsible for the laterization as such. They present, however, the opportunity for a detailed study of the different phases of laterization by their continuously bringing fresh

and unlaterized soil material (of a ' braunlehm ' or ' rotlehm ' character) into the cavities of the mature laterite layer. They and the termites are, however, responsible for the vermicular structure of some laterites.

MR. D. H. MURPHY: How far are chemical processes responsible for the migration of silica affected by, or even to some extent caused by, microbial activity, and am I right in thinking that bacteria are often instrumental in the mobilization of other components such as calcite, iron hydroxide and humus ?

PROFESSOR KUBIENA: I think that in terrestrial soils the formation of silica and iron hydroxide is mainly produced by purely chemical processes. In the translocation within the soil profile, earthworms may sometimes play an important role which gains particular significance in the enrichment of upper soil horizons with lime in certain soils (the formation of ' tangel ' humus in rendzinas, enrichment of non-calcareous sediments with lime which are underlain by marl in the Mediterranean countries *etc*). One concludes from the investigation of thin sections that humification is primarily produced in the animal body, although one can sometimes observe a striking deep brown darkening of organic residues rich in nitrogen (production of ' melanine humus ') outside the coprogenic part of the humus formation directly attacked by actinomycetes. In subaqueous soil formations calcium carbonate is, with some exceptions, biogenetically formed. This is partly the case with silica and iron hydroxide. In an early paper I stated the presence of active iron bacteria in a semi-terrestrial soil; this has been regarded by Cholodny as the first and only evidence of this.